as possible. After a preliminary delineation of *R. canadensis* as an essentially smooth blackberry, he combined *R. elegantulus* with it as only "a small and usually slender phasis" (see Bailey loc. cit. p. 475). The Grand Manan plants present a particular problem because they combine the prickliness of *R. elegantulus* and *R. amicalis* with the features that are commonly associated with *R. canadensis* including large size and strongly racemose inflorescences. Except for the degree of prickliness, most of the bigger plants certainly resemble *R. canadensis*.

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# CYTOLOGICAL OBSERVATIONS OF POLYGALA IN EASTERN NORTH AMERICA

WALTER H. LEWIS AND SHIRLEY A. DAVIS[1]

For a genus of over 450 species, of which no fewer than 200 are described in North and Central America, only 15 species of *Polygala* have been studied cytologically. No New World species are included in this meager total.

Unfortunately, the *Polygala* material is not particularly favorable for study. At meiosis the greatest difficulty is the low number of pollen mother cells formed in each anther, giving few figures for observation when a satisfactory stage is obtained. Under these circumstances, we have found that much more fixed bud material must be

collected for results than is usual for most genera. When to this need is added the paucity of plants at any one locality, particularly for those species endemic to the Mexican highlands where the greatest number of North American species occur, it is apparent why this feature limits chromosomal research. The meiotic process also is a hindrance. Although prophase I appears to be of unusually long duration, we agree with Glendinning (1960) that diakinesis is deceptive in that some chromosomes are still very poorly stained. The most satisfactory stages between prometaphase I and telophase I, however, are completed in very short periods of time which markedly decrease the chance of locating satisfactory figures. Complete restitution nuclei are formed only to be followed in rapid sequence by the phases of meiosis II. Finally the chromosomes of most species are very small and high in number.

A list of reported chromosome numbers in *Polygala* has been compiled (Table 1). Five of the 15 species have been examined by two or more authors, but except for *P. myrtifolia* L. none of these has been given the same chromosome number. This is perhaps the best illustration of the technical difficulties to be encountered in *Polygala*. The 3 African species listed have a basic number of $x = 19$ which are according to Larsen (1959) secondary diploid species probably of tribasic origin from $6 + 6 + 7$ stocks. The single Asian species, *P. japonica* Houtt., has $n = 21$ chromosomes and may be a hexaploid species with a base of $x = 7$. As many as 73% of the European species counted have basic numbers of $x = 17$. As noted in Table 1, the reports are not unanimous for species considered in this series, but the numerous counts from several localities made by Glendinning (1960) outweigh the evidence of earlier authors. It cannot be overruled, however, that chromosmal races may exist for a single species, so that *P. amara* L. may have an $n = 14$ race in eastern Europe (Baskay, 1956; Skalińska et al., 1959) and an $n = 17$ race in western Europe (Glendinning, 1960). The remaining European species have basic numbers of $x = 7, 8,$ and 23 (Table 1).

Of other genera in the Polygalaceae records exist for only

4 species, one each in *Atroxima, Bredemeyera, Carpalobia,* and *Securidaca.* These are *A. liberica* Stapf., $2n = 18$ (Mangenot and Mangenot, 1957) *B. colletioides* Phil., $2n = 14$ (Covas and Schnack, 1946), *C. lutea* G. Don, $2n = 20$ (Mangenot and Mangenot, 1957), and *S. longipedunculata* Fres., $2n = 32$ (Mangenot and Mangenot, 1958; Miège, 1960).

## MATERIALS AND METHODS

From 39 collections of immature flower buds made from localities in the eastern United States and Mexico, chromosome numbers for 24 species of *Polygala* are reported. The buds were fixed in the field in modified Carnoy's solution (4: 3: 1) and shortly thereafter were stored in the refrigerator for periods up to 6 months before squashing in 1% acetic-orcein. The results are mostly from the study of pollen mother cells or more rarely from premeiotic mitosis. The chromosome number reported for each species is when possible based on the study of more than one plant from several localities. Voucher specimens were obtained for each collection. A complete set has been filed at the Southern Methodist University herbarium (SMU), except for a few which are deposited elsewhere as indicated in Table 2. Duplicates of most collections are filed at the University of Texas herbarium (TEX). We wish to thank the curators of these herbaria for accepting specimens for permanent accession and we especially appreciate receiving fixed material of 3 species from Dr. Robert Kral, Virginia Polytechnic Institute, Blacksburg.

## RESULTS

The gametic chromosome numbers for 24 species of *Polygala* are listed by sections (Blake, 1924) in Table 2. Most of the data are based on distinct figures giving definite counts, although the numbers for a few species are only approximations. With rare exceptions (*P. praetervisa* Chod., fig. 11), meiotic behavior was regular. The chromosomes of all species were found to be generally small with the smallest in the sections *Hebeclada* (fig. 5), *Monninopsis* (fig. 15), and *Timutua* (fig. 3, 10, 11, 14), and the largest

in the section *Timutua* (fig. 2, 7-9). Chromosomes of individual karyotypes often varied from very short to intermediate in length as shown by the mitotic chromosomes of *P. reducta* Blake (fig. 13).

The most striking result was the diversity of chromosome numbers for such a small fraction of species. Numbers ranging from $2n = 16$ for *P. scoparia* HBK. to $2n = $ ca. 104 (108) for an undescribed Mexican species related to *P. alba* Nutt. represent both the lowest and the highest numbers known in the genus. Basic numbers were equally as variable. The species are separable into a primary aneuploid series with basic numbers of $x = 6(12)$, $7(14)$, 8, and 10, and a secondary basic series of $x = 15$, 17, and 23. Probably the closely related *P. cruciata* L. and *P. chapmanii* T. & G. with $n = 18$ and 36, respectively, represent species in still another series of $x = 9$, but until further research reveals the existence of species with 9 haploid chromosomes or until some other evidence is presented, all species having chromosome multiples of 6 are grouped in the $x = 6(12)$ line.

Common to species in the sections *Monninopsis* and *Timutua*, the basic number of $x = 17$ includes about 30% of the species studied. The tetraploid species are slightly more common than the diploids. The basic number of $x = 6$ was also shared by species in these sections. Species with $x = 7$ are distributed in 3 sections, *Eurhinotropis*, *Hebeclada*, and *Timutua*, which illustrates a greater degree of morphological diversity than do species of other basic series in eastern North America. The $x = 8$ and 10 lines are represented by one species each in the sections *Monninopsis* and *Timutua*.

Since at least 4 primary basic numbers are reported for *Polygala*, the secondary dibasic and tribasic lines may have arisen in a number of ways. The $x = 15$ group, common to 2 species in the section *Microthrix*, could have formed from species with $n = 7$ and 8 or, providing stronger evidence is found for the existence of an $x = 9$ series, 6 and 9 chromosomes. In view of the chromosomal diversity recorded by this small sample, it is not inconceivable that these species are unibasic polyploids at the $6x$ and $12x$ levels of an $x = 5$

series. There is less doubt that the $x = 17$ series is of dibasic origin and it may have formed by hybridization of species with 7 and 10 or 8 and 9 haploid chromosomes. The single species with $x = 23$, *P. nuttallii* T. & G., is most probably of tribasic origin and numerous combinations exist in species of the same section to give the necessary chromosomal complement. Without experimental evidence and with only limited counts in the genus as a whole, it is far too speculative at the present time to suggest definite origins for the secondary lines.

The levels and frequencies of ploidy exhibited by the 24 North American species are summarized as follows: primary diploids, 5%; secondary diploids, 21%; primary polyploids, 53%; and secondary polyploids, 21%. Since the secondary diploids are probably all amphidiploids, this gives a total polyploid frequency of 95% or a markedly higher one than the average of 30-35% estimated for the angiosperms in general (Stebbins, 1938). These data are tabulated in Table 3 by basic chromosome number, except that species no. 4 (Table 2) is omitted.

## DISCUSSION

Although the total number of species studied is only 39, it is sufficiently large to show the importance of polyploidy in addition to hybridization and aneuploidy in the phylogeny of *Polygala*. The numerical modifications have been so extensive, however, that they have obscured the original chromosome number of the genus. The most frequent number, $x = 17$, can be derived from several primary lines and gives no direct evidence of the composition of the original complement. The numbers of $x = 7, 8, 9,$ and 10, in four

FIGURES 1-16. Chromosomes of *Polygala*, drawn with the aid of a camera lucida at × 2300 reduced by ca. 1/3 in reproduction. Fig. 1. *P. alba*, $n = 12$, *Lewis 5537*; fig. 2. *P. chapmanii*, $n = 36$, *Lewis 5690*; fig. 3. *P. cruciata*, $n = 18$, *Lewis 5692*; fig. 4. *P. curtissii*, $n = 20$ (1 side of metaphase II), *Kral 13817*; fig. 5. *P. grandiflora*, $n = 14$, *Lewis 5680*; fig. 6. *P. scoparia*, $2n = 16$, *Lewis 5753*; fig. 7. *P. mariana*, $n = 17$, *Lewis 5625*; fig. 8. *P. nana*, $n = 34$, *Lewis 5654*; fig. 9. *P. nuttallii*, $n = 23$, *Kral 13791*; fig. 10. *P. polygama* var. *obtusata*, $n = 28$, *Lewis 5621*; fig. 11. *P. praetervisa*, $n = 48$ (as 46II + 1III + 1I), *Lewis 5667*; fig. 12. *P. ramosa*, $n = 34$ (1 side of anaphase I), *Lewis 5691*; fig. 13. *P. reducta*, $2n = 30$, *Lewis 5757*; fig. 14. *P. rugelii*, $n = 34$, *Lewis 5681*; fig. 15. *P. scoparioides*, $n = 17$, *Lewis 5545*; fig. 16. *P. verticillata* var. *isocycla*, $n = 17$ (1 side of metaphase II), *Lewis 5628*.
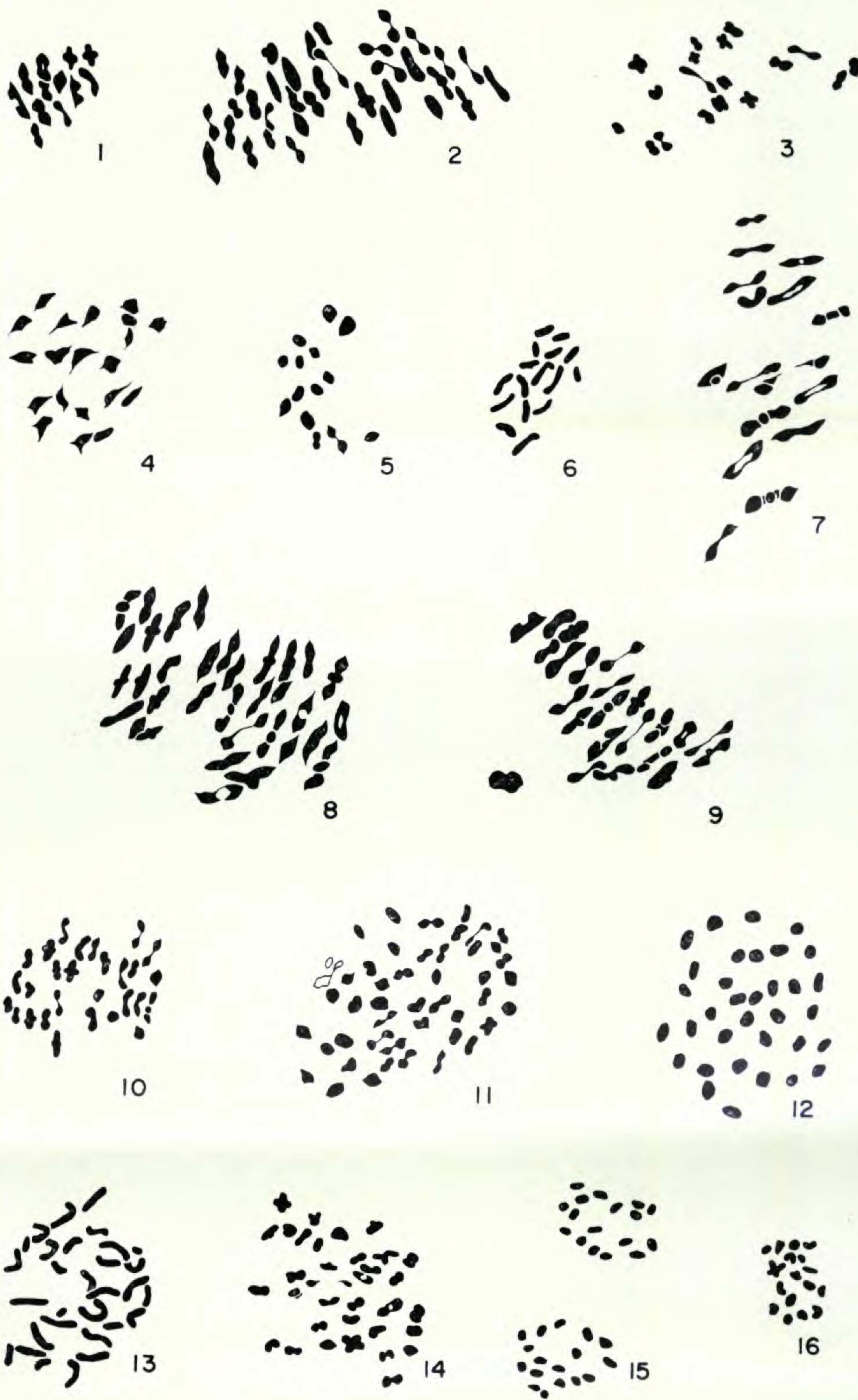
other polygalaceous genera are too limited to suggest a trend. Even though the series with $x = 7$ includes just 7 species, they are native to Asia, Europe, and North America, to give in total the most extensive distribution of any series. In addition, these species are classified in 5 sections and represent the most diverse morphology of any series. Further research may suggest a different conclusion, but the evidence now available supports $x = 7$ as the original basic number for *Polygala* and probably for the family. The origin of the $x = 6$ line can be postulated on the basis of chromosomal loss and the $x = 8, 9(?)$, and 10 groups by chromosomal gain from 7.

A suggestion of the antiquity of the primary aneuploid lines is found in the widespread occurrence of the $x = 17$ stock in the modern flora. A majority of the European and southeastern North American species now known have this number in common. It is reasonable to speculate that the species with $x = 17$ had a single origin and that migration around the North Atlantic, when it was effectively possible in the early Tertiary (Axelrod, 1960), established the group in both continents. Alternately, the number could have arisen independently, but the chance of forming a derived stock twice with both giving rise to parallel lines of descent of about equal significance and success in two continents seems much less probable. If the $x = 17$ series had formed in either Europe or North America by the early Tertiary, then the basic aneuploid differentiation must have occurred in the Cretaceous or earlier. The great antiquity of the primary series may account to some extent for the loss of most of the diploid species (1 out of 39 species) and for the high level of polyploidy reached by the $x = 6$ ($16x$) and 7 ($12x$) groups. In the secondary aneuploid lines, unquestionably of more recent origin, about one-half of the North American species are diploids and all polyploids are only $4x$. — DEPARTMENT OF BIOLOGY, STEPHEN F. AUSTIN STATE COLLEGE, NACOGDOCHES, TEXAS.

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Table 1. Chromosome numbers reported for the Old World *Polygala*.

| Taxon | n | 2n | Author |
|---|---|---|---|
| AFRICA | | | |
| *P. myrtifolia* L. | 19 | . . | Larsen (1959) |
| *P. myrtifolia* L. | . . | ca. 38 | Glendinning (1960) |
| *P. triflora* L. | 19 | . . | Hagerup (1932) |
| *P. virgata* Thunb. var. | | | |
| *speciosa* (Sims) Chod. | . . | 38 | Larsen (1959) |
| ASIA | | | |
| *P. japonica* Houtt. | . . | 42 | Suzuka (1950) |
| EUROPE | | | |
| *P. alpestris* Rchb. | 17 | ca. 34 | Glendinning (1960) |
| *P. alpina* Perr. & Song. | . . | ca. 34 | Glendinning (1960) |
| *P. amara* L. | 14 | . . | Baksay (1956) |
| *P. amara* L. subsp. | | | |
| *amarella* Cr. | 17 | 34 | Glendinning (1960) |
| *P. amara* L. subsp. | | | |
| *brachyptera* (Chod.) Hay. | . . | 28 | Skalinska *et al.* (1959) |
| *P. calcarea* Schultz | 17 | 34 | Glendinning (1960) |
| *P. chamaebuxus* L. | . . | 38 | Mattick (1950) |
| *P. chamaebuxus* L. | 22, 23, 24 | . . | Glendinning (1955) |
| *P. chamaebuxus* L. | . . | ca. 46 | Glendinning (1960) |
| *P. comosa* Schkr. | . . | 28-32 | Mattick (1950) |
| *P. comosa* Schkr. | . . | 28 | Larsen (1956) |
| *P. comosa* Schkr. | 17 | 34 | Glendinning (1960) |
| *P. major* Jacq. | . . | 32 | Mattick (1950) |
| *P. nicaensis* Risso subsp. | | | |
| *corsica* Graebn. | . . | 34 | Contandriopoulos (1957) |
| *P. serpyllifolia* Hose. | 17 | 34 | Glendinning (1960) |
| *P. vayredae* Costa | . . | 28 | Glendinning (1960) |
| *P. vulgaris* L. | 24-28 | . . | Wulff (1938) |
| *P. vulgaris* L. | . . | ca. 70 | Löve & Löve (1944) |
| *P. vulgaris* L. | . . | 28, 32, ca. 56 | Mattick (1950) |
| *P. vulgaris* L. | 34 | 68 | Glendinning (1960) |

Table 2. Chromosome numbers for 24 North American species of *Polygala*.

| Taxon | Gametic Number (*n*) | Voucher |
|---|---|---|
| Section *Eurhinotropis* | | |
| *P. tweedyi* Britt. | ca. 14 | TEXAS. San Patricio Co., 2.1 miles NW of Mathis, *Lewis & Jones 5583* (1).[c] |
| Section *Hebeclada* | | |
| *P. grandiflora* Walt. | 14 | FLORIDA. Glades Co., 8.6 miles SE of Palmdale, *Lewis 5680* (3). |

| Taxon | Gametic Number (n) | Voucher |
|---|---|---|
| Section *Microthrix* | | |
| *P. ovatifolia* Gray | 28-30[a] | TEXAS. San Patricio Co., 2.1 miles NW of Mathis, *Lewis & Jones 5586* (1). |
| *P. reducta* Blake | 15[a] | NUEVO LEON. 15.2 miles E of Hwys. 57 and 60 junction, *Lewis 5757* (2). |
| *P. scoparia* HBK. | 8[a] | NUEVO LEON. 11 miles E of Hwys. 57 and 60 junction, *Lewis 5753* (4). |
| *P. scoparioides* Chod. | 17 | TEXAS. Brewster Co., Big Bend National Park, Chisos Mts., *Lewis 5545* (1); Panther Junction, *Lewis 5466* (1). |
| *P.* sp. (1)[b] | 12[a] | NUEVO LEON. 9.9 miles E of Hwys. 57 and 60 junction, *Lewis 5746* (1, US). |
| Section *Timutua* | | |
| *P. alba* Nutt. | 12 | TEXAS. Brewster Co., Big Bend National Park, *Lewis & Oliver 5455* (2); Culberson Co., North McKittrick Canyon, *Lewis 5537* (2). |
| *P. boykinii* Nutt. | ca. 14[a] | FLORIDA. Dade Co., Homestead, *Lewis 5676* (1). |
| *P. chapmanii* T. & G. | 36 | MISSISSIPPI. Hancock Co., 0.5 miles W of St. Louis Bay & Hwy. 90, *Lewis 5690* (2). |
| *P. cruciata* L. | 18 | MISSISSIPPI. Hancock Co., 6.2 miles ENE of Pearl River and Hwy. 90, *Lewis 5692* (3); VIRGINIA. Brunswick Co., 10.5 miles WNW of Emporia, *Kral 13633* (2, VPI). |
| *P. curtissii* Gray | 20 | VIRGINIA. Southampton Co., 8 miles E of Emporia, *Kral 13817* (2, VPI). |
| *P. lutea* L. | 34 | MISSISSIPPI. Hancock Co., 0.5 miles W of St. Louis Bay and Hwy. 90, *Lewis 5689* (1). |
| *P. mariana* Mill. | 17 | TEXAS. Hardin Co., Kountze Lookout Tower, *Lewis 5629* (2); Jasper Co., 50 yds. S of Hwys. 96 and 1004 junction, *Lewis 5625* (1); Polk Co., 3 miles SW of Barnum, *Lewis 5633* (2); San Augustine Co., 0.7 miles SW of Boykin Spring entrance and Hwy. 63, *Lewis & Oliver 5511* (1). |
| *P. nana* (Michx.) DC. | 34 | FLORIDA. Citris Co., 0.4 miles N of Citris Co.-Hernando Co. line and Hwy. 19, *Lewis 5654* (2); TEXAS. Jasper Co., |

| Taxon | Gametic Number ($n$) | Voucher |
|---|---|---|
| | | 50 yds. S of Hwys. 96 and 1004 junction, *Lewis 5623* (2); Newton Co., 4.7 miles S of Newton, *Lewis 5619*. |
| *P. nuttallii* T. & G. | 23 | VIRGINIA. Nansemond Co., N of Cleopus, *Kral 13791* (1, VPI). |
| *P. polygama* Walt. var. *polygama* | 28 | TENNESSEE. Polk Co., 1 mile N of Hwys. 64 and 30 junction, *Lewis 5640* (1). |
| *P. polygama Walt.* var. *obtusata* Chod. | 28 | GEORGIA. Henry Co., 10 miles N of Griffen, *Lewis 3648* (3); TEXAS. Hardin Co., 1.4 miles SE of Votaw, *Lewis 5631* (2); Newton Co., 2.5 miles N of Burkeville, *Lewis 5616* (1), 2.8 miles S of Newton, *Lewis 5621* (1). |
| *P. praetervisa* Chod. | 48 | FLORIDA. Monroe Co., Big Pine Key, *Lewis 5667* (1). |
| *P. ramosa* Ell. | 34 | MISSISSIPPI. Hancock Co., 6.2 miles ENE of Pearl River and Hwy. 90, *Lewis 5691* (4). |
| *P. rugelii* Shuttlw. | 34 | FLORIDA. Glades Co., 8.6 miles SE of Palmdale, *Lewis 5681* (1). |
| *P. verticillata* L. var. *isocycla* Fern. | 17 | TEXAS. Hardin Co., Kountze Lookout Tower, *Lewis 5628* (3); Nocogdoches Co., 0.6 miles E of Martinsville, *Lewis 5723* (1); Panola Co., 2.3 miles NE of Pinehill, *Lewis 5720* (2). |
| *P.* sp. (2)[b] | ca. 42[a] | NUEVO LEON. 11 miles E of Hwys. 57 and 60 junction, *Lewis 5754* (1, US). |
| *P.* sp. (3)[b] | ca. 36 | OAXACA. N of Huaguapan de Leon, *Oliver 136* (1, US). |
| *P.* sp. (4)[b] | 52-54[a] | COAHUILA. 3.1 miles N of Los Llanos, *Lewis 5728* (2, US). |
| *P.* sp. (4) | ca. 52[a] | NUEVO LEON. 15.2 miles E of Hwys. 57 and 60 junction, *Lewis 5755* (1, US). |

[a] Based on the somatic number of premeiotic cells.
[b] Probably represent new species to be discussed in a subsequent paper.
[c] Number of plants examined for the chromosome number.

Table 3. Basic chromosome numbers and levels of ploidy with numbers of species by sections for 23 North American species of *Polygala*.

| Basic number | Ploidy | Number of species | Section |
|---|---|---|---|
| $x = 6$ | 4x | 2 | *Monninopsis, Timutua* |
| | 6x | 1 | *Timutua* |

|         |      |   |                                          |
|---------|------|---|------------------------------------------|
|         | 12x  | 2 | *Timutua*                                |
|         | 16x  | 1 | *Timutua*                                |
| x = 7   | 4x   | 3 | *Eurhinotropis, Hebeclada, Timutua*      |
|         | 8x   | 1 | *Timutua*                                |
|         | 12x  | 1 | *Timutua*                                |
| x = 8   | 2x   | 1 | *Monninopsis*                            |
| x = 10  | 4x   | 1 | *Timutua*                                |
| x = 15  | 2x   | 1 | *Microthrix*                             |
|         | 4x   | 1 | *Microthrix*                             |
| x = 17  | 2x   | 3 | *Monninopsis, Timutua*                   |
|         | 4x   | 4 | *Timutua*                                |
| x = 23  | 2x   | 1 | *Timutua*                                |

## SYNTHESIS OF ASTER HERVEYI

### Leonard J. Uttal

Long suspected to be a hybrid between *Aster spectabilis* Ait. and *A. macrophyllus* L.[1], *A. Herveyi* Gray can now be reported as so in fact. The putative parents have been artificially crossed and resulting progeny compare satisfactorily with naturally occurring *A. Herveyi*. Subsequent reference to this plant will be as *A.* × *Herveyi* Gray.

*A. spectabilis* is a coastal plain species from Massachusetts to South Carolina[2]. *A. macrophyllus* is a species of the eastern North American upland. The two are allopatric except in a few counties of southeastern New England and eastern Long Island. Here the two ranges impinge ecologically and physiographically, and here occur the hybrid swarms of *A.* × *Herveyi*. A specimen from Plainfield, New Jersey collected in 1909, now in the New York Botanical Garden Herbarium, indicates that sympatry between the parent species existed in parts of the New York metropolitan area before its development.

*A. spectabilis* and *A. macrophyllus* are both present in the

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[1]Fernald, M. L. 1950. Gray's Manual of Botany, 8th. Ed.: 1430.

[2]Southern limit based on information from North Carolina herbaria. (Harry E. Ahles, pers. com.)